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New records of little-known species of *Carbomyces* (*Carbomycetaceae*, *Ascomycota*)

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abstract— The genus *Carbomyces* is reported for the first time for the Mexican mycobiota. *Carbomyces emergens*, *C. gilbertsonii,* and *C. longii* were collected in the Chihuahuan desert, Mexico. *Carbomyces emergens* was more frequently collected and more widely distributed, while *C. gilbertsonii* and *C. longii* each have a restricted distribution and represent second records worldwide. The phenology, chorology, and macro-/microscopic characters (including spore ornamentation by SEM) are outlined for all species.

Key words— *Pezizales*, taxonomy, truffles

Introduction

Several collections of hypogeous and semi-hypogeous species have been recorded in recent studies of gasteroid and secotioid fungi in Chihuahua State, including the central Chihuahuan desert, Mexico (Lizárraga et al. 2010; Moreno et al. 2010). Fungi reported here were found on the soil surface and wrongly considered in situ to represent basidiomycetes. However, careful examination revealed that these fungi represent two different ascomycete species in the genus *Carbomyces* Gilkey.

Hypogeous ascomycetes, which are widely distributed, occur in different forest types (e.g., coniferous dominated by *Pinaceae,* angiospermous with *Betulaceae*, *Salicaceae*, *Fagaceae*, and *Myrtaceae*). Some even associate with herbaceous plants and shrubs, such as those in the *Cistaceae*. Cistaceous plants found in arid areas of the Mediterranean basin, southern Europe, northern

Africa, and the Middle East play an important role in plant conservation by protecting sensitive areas from erosion from heavy rain and human activity. In these areas, cistaceous plants can form mycorrhizal associations with several different fungal genera such as *Choiromyces*, *Picoa*, *Terfezia*, *Tirmania*, and *Tuber.*

However, in America, *Cistaceae* does not occur and arid lands are commonly dominated by *Cactaceae*, *Fouquieriaceae*, *Mimosaceae,* and *Zygophyllaceae*. *Carbomyces* was described from deserts of New Mexico and California (USA) for *C. emergens* and *C. longii* by Gilkey (1954), who published macro- and microscopical drawings of both species (Gilkey 1955).

Trappe & Weber (2001) later described in detail those two species and transferred a third species, *C. gilbertsonii*, into *Carbomyces* from the puffball basidiomycete genus *Abstoma* G. Cunn. where it had previously been misplaced (Zeller 1944). These truffles appear endemic to North American deserts, occurring in the Chihuahuan, Sonoran, and Mohave deserts from New Mexico to southern California, where they appear from September through April. *Carbomyces,* which is adapted to extreme xeric conditions, differs from other hypogeous ascomycetes in globose emergent ascomata, a two-layered peridium, and a powdery gleba at maturity resulting from the disintegrated asci (a feature also shared with *Elaphomyces* spp. and *Ruhlandiella berolinensis* Henn.).

Most specimens have been found ex situ since they are easily wind-blown when mature (lying dry and loose) or eaten and transported (when immature?) by rodent mycophagists (Zak & Whitford 1986), so that fungal populations can be easily intermixed and subsequently confused. Nevertheless, in the Chihuahuan desert (Mexico), we found pure (i.e. non-intermixed) populations in situ that appeared macroscopically very similar, to other known species based on spore ornamentation (smooth vs. rough) and shape (ellipsoid vs. globose).

Gilkey (1954) placed *Carbomyces* in the *Terfeziaceae*, but Trappe (1971) erected the monotypic *Carbomycetaceae* for the genus, a taxonomic position later accepted by several authors (Trappe 1979, Trappe & Weber 2001, Lumbsch & Huhndorf 2007). Nevertheless, the true relationship between *Carbomyces* and other ascomycetes was unknown until recently (Hansen & Pfister 2006). The putatively non-mycorrhizal genus *Carbomyces* is thought to be ectomycorrhizal (ECM), although no ECM hosts have been identified in its natural habitat (Trappe 1971; Zak & Whitford 1986; Trappe & Weber 2001).

In the present work all three *Carbomyces* species —*C. emergens, C. gilbertsonii, C. longii*— are reported from Mexico for the first time and redescribed from recently collected specimens.

Materials & methods

The ascocarps were studied in situ following general methods (Cifuentes et al. 1986, Moreno & Manjón 2010). Dried material was studied at the lab using KOH 5%,

Melzer's reagent (MLZ), Cotton blue (CB), Congo red 1%, and Hoyer's medium for microscopical observations. A Nikon Eclipse 80i phase-contrast microscope was used for spore measurements (on dead dried material) under oil immersion including surface structures such as spines or warts (on 25 spores).

Spore ornamentation was also studied under a scanning electron microscope Zeiss DSM 950. Critical point drying technique was performed on the samples prior to mounting, following Moreno et al. (1995).

The collections are kept in the Herbarium UACJ of the "Departamento de Ciencias Básicas, Universidad Autónoma de Ciudad Juárez," Mexico, with duplicate sets in Herbarium AH of the Universidad de Alcalá de Henares and the macromycetes collection of the Centro de Estudios Superiores del Estado de Sonora (CESUES).

High-quality DNA extract could be obtained from only one fruiting body of *Carbomyces emergens* (AH 39344), probably due to the extreme climatic conditions and high temperatures over long periods to which the other samples were naturally exposed. DNA extraction and PCR protocols followed Checa et al. (2012). ITS (JQ023163) and 28S nLSU (JQ023164) regions were sequenced, deposited in GenBank, and aligned with their closest BLAST matches from sequences deposited by Ferdman et al. (2005), Hansen et al. (2001, 2005), Trappe et al. (2010), and others.

Taxonomy

Carbomyces emergens Gilkey, N. Amer. Fl., Ser. 2, 1: 27 (1954) Figs 1–3, 11–13

Ascomata subglobose, ovoid to pyriform, 1.2–3 × 1.5–4.4 cm, scattered or occasionally in small groups. Peridium coriaceous, two-layered: outer layer very thin, membranous, initially whitish but finally yellow-brownish to dirty greyish, firmly attached, cracking by fissures or polygonal plates; inner layer ochraceous to dark brown, 0.2–0.6 mm thick. Gleba multilocular, although apparently seeming to be solid, dark brown with sterile, lighter veins forming a fragile reticule; spore mass pulverulent, dark with olivaceous or vinaceous tints. Asci globose to subglobose or ovoid, 8-spored, 40–55 × 30–5 µm, with thin brownish walls disintegrating at maturity. Ascospores hyaline to light yellowish, globose, inamyloid, 9–14 µm diam., having a thick wall (1.2–1.5 µm) finely punctate when fully mature (as seen at 400× under LM, feebly verrucose under the SEM), but appearing smooth when immature.

Specimens examined: **MEXICO, Chihuahua**: **Municipality of Juárez**, in arid land: 20.IV.2005 R. Silva (UACJ 06); km 30 road Ciudad Juárez to Casas Grandes, next *to Larrea tridentata* Coville, 3.VIII.2008 M. Lizárraga, H. Pelayo (UACJ 1166 in AH 39344; GenBank Acc. Nos.—ITS: JQ023163, LSU: JQ023164); 31°23'20.21"N 106°23'32.94"W, alt. 1312 m, 27.III.2010, M. Lizárraga, M. Vargas, D. López (UACJ 1555); 8.V.2010 M. Lizárraga, D. López, F. Félix, M. Vargas (UACJ 1556); 15.IX.2010 (UACJ 1684); 6.XI.2010 M. Vargas, M. Lizárraga (UACJ 1687); 31°22'47.44"N 106°24'3.89"W, alt. 1319 m, 22.X.2010 (UACJ 1688; 30.X.2010 (UACJ 1700); 6.XI.2010 (UACJ 1689); 31°20'13.47"N 106°23'32.95"W, alt. 1334 m, 15.V.2010 M. Vargas, F. Félix, M. Lizárraga, D. López (UACJ 1686); 15.IX.2010 M. Vargas, M. Lizárraga (UACJ 1685); 10.IV.2011 (UACJ 1683); 31°19'39.98"N 106°30'7.43"W, alt. 1280 m, 23.V.2010 M. Lizárraga, D.

López, M. Vargas (UACJ 1557); 2.X.2010 M. Lizárraga, M. Vargas, D. Sáenz (UACJ 1628). **Municipality of Ojinaga**, La Mula, 29°14'24.0"N 104°26'09.0"W, alt. 1380 m, 24.V.2009 M. Lizárraga, C. Salazar, D. Sáenz, D. López, A. Gutierrez, E. Hernández (HM 22 in CESUES 7550); 24.X.2009 M. Lizárraga, A. Sánchez, A. Gutierrez, C. Salazar, D. López (HM 171 in CESUES 7551).

Remarks— *Carbomyces emergens* has been repeatedly described (e.g., Trappe & Weber 2001) as having smooth or minutely roughened ascospores, but our studies show they are clearly warted at or above 400×. This may be because fully mature ascomata had not been found until now. The species could be macroscopically confused with *C. longii* and *C. gilbertsonii*, which share a similar habitat, but the species are easily differentiated by shape and spore ornamentation. Small sporocarps of *C. emergens* could easily be misidentified in situ as species of the basidiomycete genus *Arachnion* Schwein. (*Agaricaceae*) but in *Arachnion* the gleba lacks ascal remnants and contains a capillitium, and small (< 6 µm diam.) verrucose spores.

Zak & Whitford (1986) described the hypogeous development of *Carbomyces emergens* and reported the ascomata's apparent ingestion by rodents after collecting a few dried sporocarps in Northern Chihuahuan desert. Despite firm evidence, they suggested that fruiting probably occurs during late winter (January–March). Our collections UACJ 06 and UACJ 1557 are assumed to be immature, while the remaining specimens show an evident mature development.

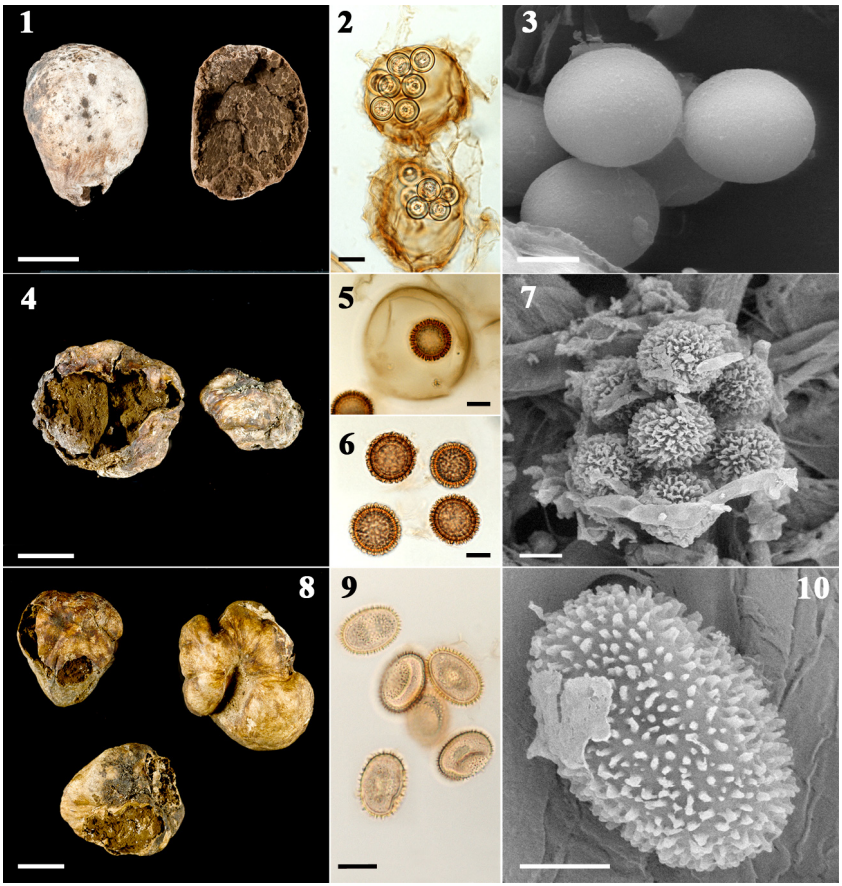
Trappe & Weber (2001) regard *C. emergens* as the most common and widely distributed *Carbomyces* species, although reported only from American Southwest —Arizona, California, and New Mexico. Here we report it for the first time in Mexico as an apparently common species of the central Chihuahuan desert.

Carbomyces gilbertsonii N.S. Weber & Trappe, Harvard Pap. Bot. 6: 212 (2001) [nom. nov.] Figs 4–7, 14–16

≡ *Abstoma longii* Zeller, Mycologia 36: 628 (1944) [non *Carbomyces longii* Gilkey]

Ascomata immersed and finally superficial, globose to subglobose, laterally compressed to irregular, 2–3 cm diam. Peridium two-layered, mostly persistent, ferruginous at maturity. Gleba solid, pulverulent, brown to dark brown. Asci subglobose, 8-spored, 40–65 µm diam., with thin light brown walls disintegrating at maturity. Ascospores hyaline to brownish with age, globose to subglobose, inamyloid, 20–25 µm, ornamented with spine-like elements up to 2 µm long (LM). Under SEM such "spines" consist in small clumps of slender apically fused baculae, forming pyramids with hollow bases.

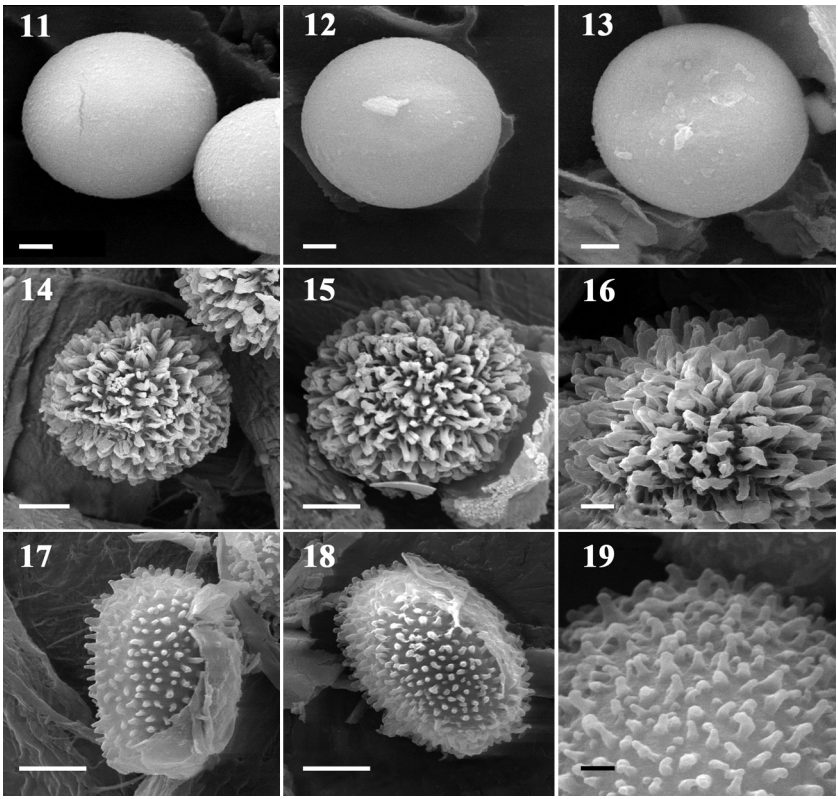
Specimens examined: **MEXICO, Chihuahua: Municipality of Juárez**, 31°22'47.44"N 106°24'3.89"W, alt. 1319 m, in arid soil near to *Larrea tridentata*, *Prosopis* sp. and *Opuntia* sp., 23.X.2010 M. Lizárraga, M. Vargas, (UACJ 1559, duplicate in AH 39346);



Figs. 1–3: *Carbomyces emergens* AH 39344: 1. Ascocarps. 2. Asci with spores. 3. Spores (SEM). Figs. 4–7 *Carbomyces gilbertsonii* AH 39347: 4. Ascocarps. 5. Asci with spores. 6. Free spores. 7. Spores (SEM). Figs. 8–10 *Carbomyces longii* AH 39345: 8. Ascocarps. 9. Free spores. 10. Spore (SEM). Scale bars: 1, 4, 8 = 1 cm; 2, 5, 6, 9 = 10 µm; 3, 10 = 5 µm; 7 = 10 µm.

6.XI.2010, (UACJ 1561 in AH 39347); (UACJ 1691); 31°23'20.21"N 106°23'32.94"W, alt. 1312 m, (UACJ 1690); 31°22'21.46"N 106°33'59.26"W, alt. 1225 m, 26.III.2011 (UACJ 1689).

Remarks— *Carbomyces gilbertsonii* could be macro- and microscopically confused with *C. longii*, but small, ellipsoid spores (17–19 × 12–13 µm) distinguish the latter species. Old *Scleroderma cepa* specimens could be confused with *C. gilbertsonii* specimens without ascal remains, but the smaller (9–12 µm) spores of *S. cepa* spores are diagnostic. It is noteworthy that



Figs. 11–13: *Carbomyces emergens* AH 39344: spores (SEM. Figs. 14–16 *Carbomyces gilbertsonii* AH 39347: 14–15. Spores (SEM); 16. Spore ornamentation (detail, SEM). Figs. 17–19 *Carbomyces longii* AH 39345: 17–18. Spores under SEM. 19. Spore ornamentation (detail, SEM). Scale bar: 11–13, 16 = 2 µm; 14–15, 17–18 = 5 µm; 19 = 1 µm.

C. gilbertsonii was previously known only from the type locality (New Mexico, U.S.A.); our collections add Chihuahua (Mexico) to its distribution.

Carbomyces longii Gilkey, N. Amer. Fl., Ser. 2, 1: 27 (1954) Figs 8–10, 17–19

Ascomata subglobose, laterally compressed, pyriform to irregular, 2–3 cm diam., 2.5–3 × 1.5–2 cm. Peridium two-layered, persistent, outer layer white to greyish, later light brown to dark brown with reddish tinges at maturity. Gleba pulverulent, dark brown to brown, becoming olivaceous. Asci evanescent, only a few fragments of brownish, disintegrated walls were seen. Ascospores light yellowish, ellipsoid, 17–19 × 12–13 µm, inamyloid, ornamented with regularly

distributed spines ≤ 1 µm long (LM). Under SEM, the spines are scattered, usually with bent apices.

Specimens examined: **MEXICO, Chihuahua: Municipality of Ahumada**, 31°07'32.0"N 106°29'48.0"W, alt. 1280 m, in soil next to *Larrea tridentata*, 24.VII.2009 M. Lizárraga, C. Salazar, D. Sáenz, D. López, A. Gutierrez, E. Hernández (UACJ 1699). **Municipality of Juárez**, 31°23'20.21"N 106°23'32.94"W, alt. 1312 m, 27.III.2010 M. Lizárraga, M. Vargas, D. López (UACJ 1557 in AH 39017); 3.V.2010 (UACJ 1698); 15.V.2010 M. Lizárraga, D. López, M. Vargas, F. Félix (UACJ 1558); 15.IX.2010 M. Lizárraga, M. Vargas (UACJ 1697); 22.X.2010 (UACJ 1696); 6.XI.2010 (UACJ 1694); 31°22'47.44"N 106°24'3.89"W, alt. 1319 m, 30.X.2010 (UACJ 1562, duplicate in AH 39345); 6.XI.2010 (UACJ 1693); 31°22'21.46"N 106°33'59.26"W, alt. 1225 m, 26.III.2011 (UACJ 1695).

Remarks— Since *C. longii* asci are fully evanescent, mature sporocarps could be confused with *Arachniopsis albicans* Long (*Agaricaceae*), but the latter is distinguished by small (3–5 × 3–4 µm) oval feebly verrucose basidiospores and a hyaline capillitium. Co-occurring with *C. gilbertsonii*, *C. longii* was previously known only from the type locality (New Mexico, U.S.A.). Our report from Chihuahua, Mexico, represents the second world record.

Key to *Carbomyces* species in the Chihuahuan desert, Mexico

1 Spores globose and smooth to subsmooth (LM) or feebly warted (SEM) ....*C. emergens*

1' Spores spiny 2

2 Spores ellipsoid, scattered spines ..... *C. longii*

2' Spores globose to subglobose, spines in small clumps forming pyramids .....*C. gilbertsonii*

Molecular results

28S nLSU alignment comprised 39 sequences with 215 variable sites among 563 bases, 133 of them parsimony-informative. Bayesian and parsimony analyses were generally consistent with each other (Fig. 20) and supported the three main groups already recognized in Læssøe & Hansen (2007). The first group comprises *Kalaharituber*, *Iodowynnea*, *Hydnotryopsis*, *Sarcosphaera*, and several *Peziza* spp. The second group includes *Mattirolomyces*, *Elderia*, and a different set of *Peziza* spp. The third group includes *Terfezia*, *Tirmania*, *Mycoclelandia*, *Ulurua*, *Eremiomyces*, *Ruhlandiella*, *Hapsidomyces*, *Plicaria*, and a third set of *Peziza* spp. The analyses show *Carbomyces* as somewhat related to *Kalaharituber* (*Pezizaceae*) in the first group (Fig. 20), partially confirmed by BLAST of the only ITS sequence obtained, which linked *C. emergens* to *Terfezia* and *Kalaharituber* (84% and 83% identity in 68% and 65% coverage, respectively), in accordance with data obtained by Karen Hansen (pers. comm.).

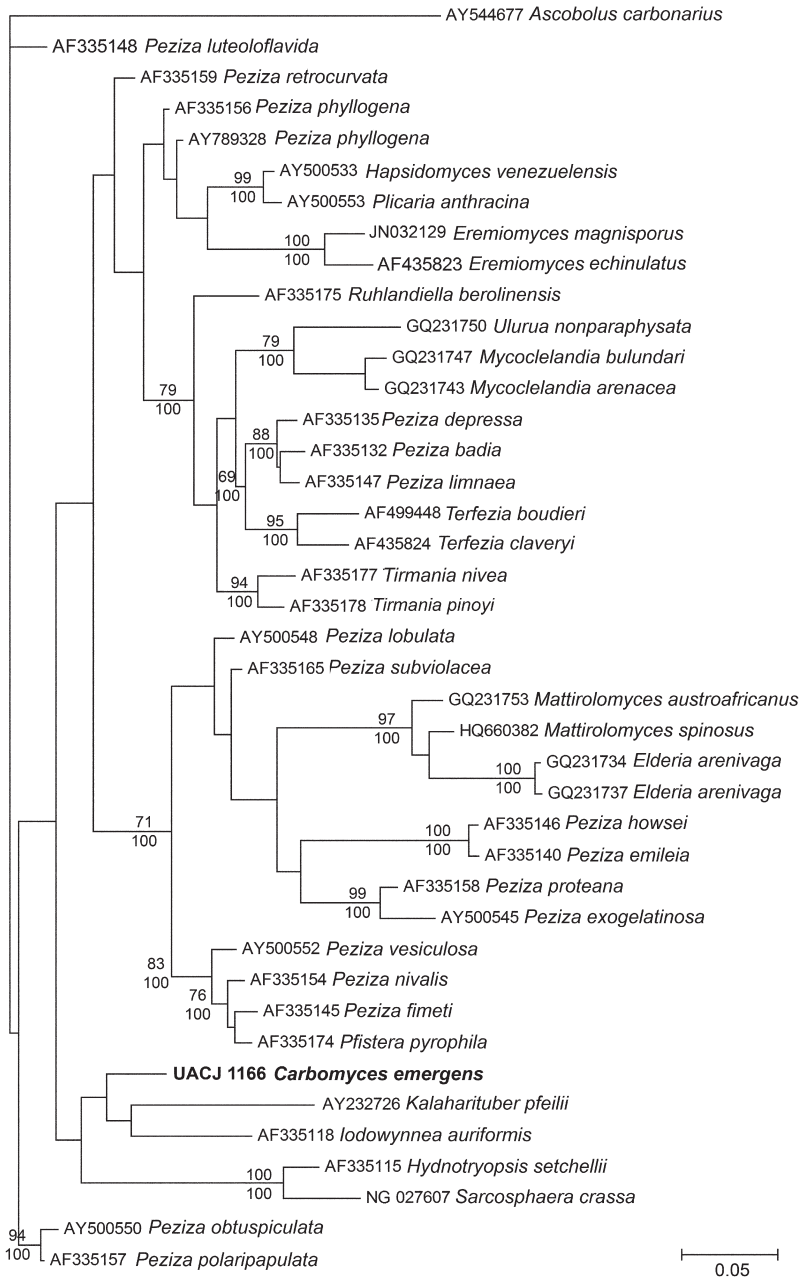

AY544677 Ascobolus carbonarius
AF335148 Peziza luteoloflavida
AF335159 Peziza retrocurvata
AF335156 Peziza phyllogena
AY789328 Peziza phyllogena
99
100
AY500533 Hapsidomyces venezuelensis
AY500553 Plicaria anthracina
100
100
JN032129 Eremiomyces magnisporus
AF435823 Eremiomyces echinulatus
AF335175 Ruhlandiella berolinensis
79
100
GQ231750 Ulurua nonparaphysata
GQ231747 Mycoclelandia bulundari
GQ231743 Mycoclelandia arenacea
79
100
88
100
AF335135 Peziza depressa
AF335132 Peziza badia
69
100
AF335147 Peziza limnaea
95
100
AF499448 Terfezia boudieri
AF435824 Terfezia claveryi
94
100
AF335177 Tirmania nivea
AF335178 Tirmania pinoyi
AY500548 Peziza lobulata
AF335165 Peziza subviolacea
97
100
GQ231753 Mattirolomyces austroafricanus
HQ660382 Mattirolomyces spinosus
100
100
GQ231734 Elderia arenivaga
GQ231737 Elderia arenivaga
71
100
100
100
AF335146 Peziza howsei
AF335140 Peziza emileia
99
100
AF335158 Peziza proteana
AY500545 Peziza exogelatinosa
AY500552 Peziza vesiculosa
83
100
76
100
AF335154 Peziza nivalis
AF335145 Peziza fimeti
AF335174 Pfistera pyrophila
UACJ 1166 Carbomyces emergens
AY232726 Kalaharituber pfeilii
AF335118 Iodowynnea auriformis
100
100
AF335115 Hydnotryopsis setchellii
NG 027607 Sarcosphaera crassa
94
100
AY500550 Peziza obtuspiculata
AF335157 Peziza polaripapulata
0.05

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Fig. 20: 28S nLSU consensus phylogram constructed in MrBayes 3.1 showing the most probable relationships between *Carbomyces emergens* and its closest relatives in the *Pezizaceae*. Numbers close to nodes represent maximum parsimony bootstrap proportions (upper), and Bayesian posterior probabilities (lower). Only nodes supported by at least one inference method were annotated.

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